

- Taylor, R. H. 1975. Some ideas on speciation in New Zealand parakeets. *Notornis* 22: 110-121.
- Warham, J. 1962. The biology of the Giant Petrel *Macronectes giganteus*. *Auk* 79: 139-160.
- 1963. The Rockhopper Penguin, *udyptes chrysocome*, at Macquarie Island. *Auk* 80: 229-256.
- 1967. The White-headed Petrel *Pterodroma lessoni* at Macquarie Island. *Emu* 67: 1-22.
- 1971. Aspects of the breeding behaviour of the Royal Penguin *udyptes chrysolophus schlegeli*. *Notornis* 18: 91-115.
- 1972a. Breeding seasons and sexual dimorphism in the Rockhopper Penguin. *Auk* 89: 86-105.
- 1972b. Aspects of the biology of the Erect-crested Penguin *udyptes sclateri*. *Ardea* 61: 145-184.
- 1974. The breeding biology and behaviour of the Snares Crested Penguin. *J. Roy. Soc. N.Z.* 4: 63-108.
- 1975. The Crested Penguins. pp. 189-269 in *The Biology of Penguins*. Macmillan, London.
- Warham, J., Keeley, B. R. & Wilson, G. J. 1977. The breeding of the Mottled Petrel *Pterodroma inexpectata*. *Auk* 94: 1-17.
- Warham, J. & Bell, B. D. 1979. The birds of Antipodes Island, New Zealand. *Notornis* 26: 121-169.
- Weller, M. W. 1972. Ecological studies of Falkland Islands' waterfowl. *Wildfowl* 23: 25-44.
- 1975. Ecological studies of the Auckland Islands Flightless Teal. *Auk* 92: 280-297.
- Williams, A. J., Siegfried, W. R., Burger, A. E. & Berruti, A. 1977. Body composition and energy metabolism of moulting eudyptid penguins. *Comp. Biochem. Physiol.* 56A: 27-30.
- Woods, R. W. 1975. *The Birds of the Falkland Islands*. Anthony Nelson: Oswestry.
- Voisin, J. F. 1976. Observations sur les pétrels géants de l'île aux Cochons (Archipel Crozet). *Alda* 44: 411-429.
- Zinderen Bakker, E. M. van, Jr. 1971a. Comparative avian ecology. pp. 161-172 in *Marion and Prince Edward Islands*. Balkema: Cape Town.
- 1971b. The genus *Diomedea*. pp. 273-282 in *Marion and Prince Edward Islands*. Balkema: Cape Town.
- 1971c. A behaviour analysis of the Gentoo Penguin (*Pygoscelis papua* Forster). pp. 251-272 in *Marion and Prince Edward Islands*. Balkema: Cape Town.
- Address: Dr. John Warham, Zoology Department, University of Canterbury, Christchurch, New Zealand.

© British Ornithologists' Club

## The present status of Antarctic ornithology

by E. C. Young

### INTRODUCTION

The three essential features of the antarctic continent critical to an understanding of antarctic ornithology are its position almost exactly centred on the South Pole, with most of its land mass below latitude 70°S; its permanent cover of ice and snow with much of its periphery at sea level girdled with glaciers or fast ice; and its great isolation from other substantial land masses across notoriously desolate ocean spaces, enhanced by the circumpolar air and water circulation patterns.

Climate similarity and biogeographical links suggest that the most useful regional area for a review of Antarctica is one extending out to about the Antarctic Convergence. The Antarctic Convergence, however, falls within the circle of westerly wind patterns and related water flow, countered in a narrow band around the continent by an easterly flow. The climate of the westerly wind zones is characterized by high, steady winds, high precipitation and predominantly cloudy weather. The weather in the easterly wind zone is generally better; drier with fewer cloudy days and lighter winds,

though colder. Antarctic personnel appreciate this difference. Working conditions are much easier on most continental rookeries than on the island rookeries further north — no smell, no wind, little rain, clear skies. The real heroes in this region are those who struggle through the bogs and mists of the subantarctic islands in oiled or sodden clothing, with damp and mildewed note-books; not those in the briskly cheerful rookeries of the far south.

As one moves south the diversity of species declines, from 26 breeding species on South Georgia to just three species for study, the Adélie Penguin *Pygoscelis adeliae* and McCormick's Skua *Catbaracta macormicki* over summer and the Emperor Penguin *Aptenodytes forsteri* in winter. A bibliography of papers published since 1960 contains 562 papers; 137 general accounts of the avifauna, 274 on penguins, 76 on petrels and albatrosses and 47 on skuas. Shags, gulls, sheathbills and the smaller petrels have received little attention.

There are a number of general accounts of the antarctic avifauna in addition to a voluminous specialist literature. Murphy's (1936) two-volume *Oceanic Birds of South America* has stood as the prime source of general information on the birds of the region to this day. Since then general reviews have appeared by Falla (1964) on the distribution of birds; Stonehouse (1965) on birds and mammals; Carrick & Ingham (1967, 1970) on recent and future research areas; Austin (1968) on recent American research; Stonehouse (1975) on the biology of penguins; Watson *et al.* (1971) on species distribution and taxonomy; and Watson (1975) on a comprehensive guide to the identification, distribution and biology of antarctic and subantarctic birds. The three SCAR biology meetings provided a wealth of information, and research output of French scientists appears regularly in *L'Oiseau*. Research programmes and short reports appear annually in antarctic journals.

Antarctic ornithology is pre-eminently the study of adaptations for survival and breeding in a severe environment, above all else to cold conditions: in the maintenance and regulations of body heat, in the adjustments of breeding patterns to a short, favourable season; and for winter survival away from the land.

#### DISTRIBUTION AND TAXONOMY OF SOME ANTARCTIC SPECIES

The breeding distributions of antarctic birds is now fairly well catalogued. The map folio of Watson *et al.* (1971) showing distribution of individual species is a remarkable achievement highlighting the rapid progress made in the biological exploration of the region. These distribution records have been compiled from an enormous variety of sources, ranging from a wealth of historical records, from incidental observations from ships, from the explorations of geologists and surveyors to the systematic surveys of geographic regions. A remarkable feature is the uniformity of species across such a large area. Only 4 species are subspecifically differentiated within the geographic range covered by this review. The Snow Petrel is considered to have 2 forms, a smaller subspecies *Pagodroma nivea nivea* over most of the continent and a much larger form *P. n. major* in Adélie land with the habit of nesting in more open terrain. The Blue-eyed Shag is considered to have 3 subspecies:— *Phalacrocorax atriceps gaini* on the Antarctic Peninsula and

Scotia Arc islands, *P. a. nivalis* on Heard, and *P. a. georgianus* on South Georgia. Wilson's storm petrel has one subspecies *Oceanites o. oceanicus* on Kerguelen and other northern islands, and *O. o. exasperatus* to the south. *Eudyptes chrysolophus* has 2 distinct subspecies, *E. c. chrysolophus*, the Macaroni Penguin, widespread through the region, and *E. c. sblegeli* the Royal Penguin of Macquarie.

Apart from these 4 species all others are monotypic throughout the region or are represented by a single subspecies with others resident further to the north. The status of the skuas is not yet clearly determined. If the morphology within species is so uniform, this must indicate genetic panmixia, so that differences found in biology, behaviour and ecology represent the effect of environmental moderators. There are nevertheless substantial taxonomic problems in some antarctic species groups.

#### GIANT PETREL (OR FULMAR)

These birds, although obviously distinct from other petrels, have long been known as a most variable taxon with an immense breeding range from the New Zealand subantarctic islands to the antarctic mainland. Bourne & Warham (1966) proposed that 2 sibling species were involved: *Macronectes halli* breeding and feeding mainly to the north of the Antarctic Convergence and *M. giganteus* to the south. Both species breed on islands close to the convergence.

The central problem of the maintenance of their specific identities is not yet solved. Although the species do have different nesting preferences and breed at different times on islands where they breed sympatrically, (at Macquarie *M. halli* lays between 11 August and 6 September and *M. giganteus* from about 27 September to 19 October (Johnstone 1979)) some interbreeding has nevertheless been observed. Different laying dates and nesting habits do not seem sufficient over a long period to prevent major hybridisation. Research could usefully be carried out on species discrimination through both morphological and behavioural features. The small differences in bill and eye colour seem negligible in comparison with the large variation in size and plumage in these dimorphic species.

#### SKUAS

At no point, from the very first reviews, has there been general agreement on how the various populations of skuas should be ordered. There are 4 main problem areas.

- 1) The relationship of the skua-jaegar group (Family Stercorariidae) to the (other) gulls.
- 2) Relations between the larger forms (the skuas) and the smaller, lighter forms (the jaegers) breeding solely in the northern hemisphere.
- 3) The relations between and status of the various 'forms' of skuas breeding in the Atlantic arctic, the subantarctic and antarctic regions. Specifically, it needs to be resolved whether these different populations are conspecific, making up a single bipolar species, whether they comprise distinct species or whether some other arrangement of specific and subspecific units is most appropriate.

4) Finally, and more trivially, there is the need to settle on acceptable common names.

It is widely accepted that there are 4 species or species groups in the Stercorariidae, comprising 3 well defined species of smaller birds (the jaegers) *Stercorarius parasiticus*, *S. pomarinus* and *S. longicaudus*, all of which are easily distinguishable on the breeding grounds but only with difficulty as juveniles or in non-breeding plumage when on their southern migrations. The fourth group consists of the (Great) skuas. These are heavy, uniformly brownish-grey birds breeding on islands and coasts of the north Atlantic and throughout the southern temperate subantarctic and antarctic zones. Their enormous geographic range, among often isolated islands and coasts, and their breeding site tenacity makes species recognition dependent on comparisons of size and plumage, breeding habits, behaviour and distributional ranges, as with other allopatric populations of superspecies. It seems extraordinary that the taxonomy should be in such disarray that skuas still appear in publications under two generic names, *Stercorarius* and *Catharacta*, with preference given to the former by European authors and to the latter by American ones. Schnell (1970) could not demonstrate differences in the skeleton of jaegers and skuas beyond those related to size. Moreover, behavioural studies by Moynihan (1959) and Andersson (1973) show a common behavioural link through all 4 with a natural grouping into 2 pairs; a smaller pair, *parasiticus* and *longicaudus* and a larger pair, *pomarinus* and *skua*.

Within the skuas themselves, the basis is Hamilton, (1934) grouping into 5 subspecies. Murphy (1936) was unable to provide a definitive classification, and concluded (p. 1012) "since I cannot decide whether the skuas represent one species or four species, I am for the present arbitrarily regarding all of them as geographic races of a single species". His species was *Catharacta skua*. Much more is known now than in Hamilton's day of their distribution, biology and migrations but not enough yet apparently for firm convictions to occur, though it has come to be generally accepted that 6 forms exist, *skua*, *maccormicki*, *lonnbergi*, *antarctica*, *hamiltoni* and *chilensis*.

Sir Robert Falla had begun to re-examine the problem and was concerned with dimorphism in plumage colour, the spasmodic occurrence of 'golden' and 'reddish-cinnamon' casts to adult plumages, and the need to establish sequences of juvenile to adult plumage changes (R. A. Falla, pers. comm.), underlining his pleading that the taxonomic viewpoint should not be overlooked in any of the research on these species (Falla 1964).

Watson (1975) concluded that there are 2 species in the antarctic: *C. maccormicki* and *C. lonnbergi*, the other forms being "probably conspecific with one or the other of the [six] antarctic skuas".

Devillers (1977) provides by far the most useful recent survey of the status and taxonomy of this group. He examined 733 specimens which, taken together with distribution records, led him to conclude that 3 species were represented in the 6 forms: that *maccormicki* and *chilensis* were specifically distinct, whereas *lonnbergi*, *skua*, *antarctica* and *hamiltoni* were each subspecies of *Catharacta skua*. This paper also provides much information on the migratory patterns of the different forms and on their recognition at sea.

Although Gain (1914) had described *lonnbergi* and *maccormicki* breeding together on the South Shetlands and Antarctic Peninsula this was not confirmed until recently (Watson *et al.* 1971). Their area of overlap has been

the focus of research of a team headed by Dr. D. F. Parmalee. His study on Anvers Island (64°46'S) has shown the considerable extent of hybridization there, and from the returns of banded fledglings that not only do *macormicki* cross the Pacific equator — which has been long known — but that they apparently also migrate into the northern Atlantic, i.e., into the breeding range of the Great Skua. (See also Salomonson 1976.) This may well be the most significant study to date on skua distribution and systematic relations.

Bonner (1964) described a single trio of breeding adults of *lonnbergi* defending territories, since when Young (1978) has found such trios on South East Island of the Chathams group. Guthrie-Smith (1925) had previously described this phenomenon as common in the Stewart Islands, and further enquiry shows that it is widespread throughout the New Zealand region. It has never been recorded in *macormicki*. If, as now seems likely, cooperative breeding has a genetic basis it indicates that the New Zealand *lonnbergi* population is somewhat genetically isolated from other skuas.

#### SNOW PETREL

The Snow Petrel *Pagodroma nivea* is represented in most of its range by the smaller *P. nivea nivea*, and in one small area on the Adélie Land Coast by the larger form *P. n. major*. Isenmann (1970a), in an analysis comparing size measurements and breeding ecology of the 2 forms concluded that they were not specifically distinct, as merging seems to be present at Cape Hunter, and that the larger form has been selected to withstand the greater cooling effect of the Adélie Coast environment for birds nesting in the open. This seems an extraordinary phenomenon repaying more detailed study.

#### SHAGS

Watson (1975) grouped the various populations of southern shags into 2 species (including the Kerguelen Shag of Voisin, 1970). Not only are the King Shag *Phalacrocorax albiventer* and Blue-eyed Shag *P. atriceps* morphologically very similar, their distribution also suggests a close affinity. The former has a more circumscribed but northern distribution, and both species breed on the southern islands and straits of South America. Behn *et al.* (1955) resolved from their surveys that *P. albiventer* had spread from the Falkland Islands east and that *P. atriceps* had dispersed from the Feugian coast of Chile towards the south and west, to as far as New Zealand, as well as northwards along the Chilean coast. They found both forms were on Tierra del Fuego. They concluded nevertheless that there were 2 valid species. Devillers & Terschuren (1978) going over the same ground, recording proportions of each form and incidences of interbreeding, on the other hand consider that the 2 forms are conspecific producing a polymorphic population in their contact area. One doubts that the last word has been written on their taxonomy and distribution.

#### THE BIOLOGY OF ANTARCTIC SPECIES

#### THE ADELIE PENGUIN *Pygoscelis adeliae*

##### *Breeding biology and behaviour*

Dr. W. J. L. Sladen, who not only saw the need for markers but perfected the present safe and durable designs of flipper bands, provided a first compendium of techniques for Adélie research, in an account (1958) that has proved to be a classic study of this bird. Similar studies were later carried out by Taylor (1962), Stonehouse (1963) and Reid (1964) at the Cape Royds

and Cape Hallet rookeries. The pattern set by these authors of combining data on colony population change, breeding cycle and behaviour into a coherent whole, and the need to relate behavioural observations to seasonal patterns has been an established working rule in Antarctica from the first.

The development of a population of known-age banded birds (32,748 banded by 1968 (Sladen *et al.* 1968)) at Cape Crozier has permitted much closer analysis of biology and breeding success than hitherto possible, and this recognisable and documented population has been frequently exploited. Le Resche & Sladen (1970), for example, explored how young birds returning to the breeding rookery become more and more fully integrated within the breeding population and confirmed what had been always tacitly assumed earlier (e.g. Penney 1968), that younger birds probably contributed most to the variability in breeding behaviour seen at rookeries. Dr. D. G. Ainley, in an important study of non-breeding Adélie Penguins (1975a, b) indicated that behaviour changes with age and that older non-breeders which showed immature patterns failed to pair. Later (1978), after discovering that some 13 year-olds were still not breeding even though physiologically capable of doing so, he concluded that non-breeding in males was related to their poor nutritional reserves at the time of arrival at the rookery, which acted to reduce their pre-breeding activity. Penney (1968) set new standards for detailed observation measurement and recording of the territorial and social behaviour of the Adélie, and Spurr (1975a, b) has produced a detailed account of the social and communication behaviour of Adélie adults and chicks at the Cape Bird rookery. Spurr has also provided (1975c) a valuable account of the breeding biology of his study population over 4 seasons.

The structure of the penguin colony has attracted considerable interest in its role in climate amelioration, and in nest protection from egg and chick predation by skuas e.g. Tenaza (1971) at Cape Hallet. Oelke (1975) has extended the work of Penney and of Tenaza to individual colonies within the Cape Crozier rookery, and his results after much analysis, have related sensibly to the results of other studies on disturbance and predation. It is doubtful if one can go much further with this approach.

A fertile direction of research has been to analyse the behaviours and responses of individuals, e.g. Spurr (1974) in a study of aggressiveness. These studies rely on filming and models, which the antarctic climate positively encourages, well demonstrated by Derksen (1977), whose use of 800 hours of time-lapse photography of up to 5 pairs gave 108,000 individual frames of film for analysis of incubation behaviour, complemented by temperature data from an egg model in the nest. Photography gets around one big problem in Antarctica; 24-hour daylight allows more or less continuous bird activity, defeating even the most assiduous observer in long term studies. Müller-Schwarze (1968) had previously found that Cape Hallet birds followed a circadian activity rhythm with an activity minimum about mid-day, which Derksen could substantiate, though Yeates (1971) was not able to demonstrate activity rhythms at Cape Royds, possibly due to temperature and light regimes being less marked at that latitude. Daily cycles have now, however, been clearly established for penguins at Cape Crozier (Müller-Schwarze & Müller-Schwarze 1971) and Cape Bird (Spurr 1978) at a similar latitude to Cape Royds.

### Feeding

Emison (1968) made the first detailed study of the feeding preferences of Adélie Penguins in the Ross Sea, without slaughtering birds, by the use of a suction tube to remove samples of food from the stomach, and showed in detail that Adélies in this area in summer were taking small shoaling organisms over 15 mm in length in the upper water layers. Ainley & Emison (1972) have attempted with some success to relate food size preference to the sexual size dimorphism of this penguin. The feeding range from rookeries still needs determination, as well as the winter diet and preferences and diets in other latitudes when competing with other penguins. The uncanny ability of the sea- and ice-bound penguins to find their feeding stations and their breeding rookeries and nests each new year has excited admiration (even wonder) in all observers. Emlen & Penney (1966) have demonstrated an acute distance navigation ability. Like the phenomenon of diurnal periodicity, this facility requires rather refined experimentation for complete analysis.

### Predation

For various reasons penguins aggregate at a small number of geographic places, forming dense colonies of breeding birds. They are not only in intense competition, but also form oases of food on land for predatory and scavenging species; in the south skuas and the Leopard Seal *Hydrurga leptonyx*, and further north in addition the giant petrels *Macronectes* and the Sheathbill *Chionis minor*.

Young (1963, 1970) showed that, contrary to belief (see Maher 1966) only a small proportion of skuas breeding on Cape Royds and Cape Barne had access to the eggs and chicks of the small Cape Royds rookery; that most were independent of penguins for successful breeding, feeding entirely at sea, plunging for surface fish; and that skuas could probably not in fact be fed throughout the season at any rookery, penguins as food becoming unavailable at the time when skua chicks were placing heaviest demands on parents. These conclusions have been amply confirmed during 5 season's observational and experimental work at the much larger Cape Bird rookeries of Ross Island (Young, in prep.) Since then, Furness (1978) has provided a bioenergetic model, employing the feeding ecology and energetics of the Great Skua in Shetland, which sets high standards for antarctic work to emulate. Trillmich (1978) has re-examined the relationship between the two birds at Cape Hallett, and concluded that sufficient penguin food was available through summer at the rookery to feed at least some pairs of skuas entirely, just what proportion is uncertain. Parmalee *et al.* (1978), on the other hand, found that on Anvers Island, *lonnbergi* skuas were dependent on penguins but that *maccormicki* fed at sea and in bad ice years were not able to breed successfully. Spellerberg (1975) has reviewed the relationship between different penguins and their possible predators (Leopard Seal, Sea Lion, Killer Whale, Skua and Sheathbill), and draws a clear distinction between gross food abundance (biomass of eggs and chicks on the rookery) and food actually available to the predator.

### Adaptions to cold climates

Life in the antarctic environment requires a complex thermoregulatory apparatus. Penguins in particular require effective insulation for heat retention

at very low temperatures that can also allow radiation during periods of intense activity or during hot sunny days on the rookery. It is provided by a stocky body insulated both with subcutaneous fat and a dense plumage, coupled with radiating surfaces on the inner face of the flippers. The exposed lower leg and feet and air passages have subtle and sensitive temperature control systems. Stonehouse (1967, 1970) was very early to consider biology and morphology in relation to the temperature environment of penguin species.

Adaptation has been shown in seasonal breeding cycles, and in migrations to breeding areas. Distribution of breeding colonies in relation to geographic and climate-related factors, such as availability of snow-free ground and access to open water (Stonehouse 1963, Ainley & Le Resche 1973) is also adaptive. Open water access is critically important in first movement to the rookery and when feeding chicks. Yeates (1975) has summarised much of the present information on micro-climate, climate and breeding in the Adélie, and Spurr (1975d) has demonstrated a very precise orientation by Adélie to face into strong winds. Sladen *et al.* (1968) describe the impact of very severe winds, above 200 km/hr. Below these levels, winds were advantageous for breeding at Cape Crozier by providing clear water for feeding. Emperor and King Penguin adults, and chicks of most species, group together in huddles or creches at certain times. There is not much doubt that this is to preserve heat in the winter breeding penguins, but its causative agent in Adélie and other chicks is not established. Creching may occur in cold weather, and certainly occurs in rookeries disturbed by skuas or man. The need now is to measure the triggering levels against chick age and colony size, as can now be done in the laboratory following the successful transplanting of Adélie Penguin colonies described by Todd (1978). There is now a voluminous research record of the anatomical and physiological basis of fasting and temperature regulation in these birds, too large to be essayed in the present review.

#### SKUAS

Eklund (1961) gave the first working account of the general biology of *Catharacta maccormicki* based on a major banding programme, complementing that of Stonehouse (1956) of the feeding and breeding biology of *C. lonnbergi* at South Georgia. These two publications together with Moynihan's (1962) work on *chilensis* provided a good framework for later research and analysis.

Young's 1959/60 study (1963a, b) at Cape Royds, continued from 1964 at Cape Bird, highlighted again the vulnerability of skuas to disturbance by man and pinpointed the major cause of their low breeding success as failure to sustain the 2 chicks after hatching — a biological paradox that has subsequently received detailed study. At about the same time Le Morvan, Mougín & Prévost (1967) were working to produce an account of the ecology at Pointe Géologie (Adélie Coast), and Reid similarly was working at Cape Hallett.

At Cape Royds Spellerberg (1971a, b) provided a 4-year account of a population existing independently of penguins. The specific problem of the early loss of one of the 2 chicks hatching at skua nests has been unravelled further by Procter (1975) who concluded that "the nutritional



condition of the chicks regulates aggressive behaviour"; but he was not able to place this anachronistically intense sibling rivalry into an ecological or evolutionary context. Parmalee *et al.* (1978) found that in years with easy feeding access to the sea *maccormicki* at Anvers Island raised 2 chicks; in bad years none. Young (1972) drew attention to the remarkable stability of skua territories. Wood's (1971) is the first paper from Cape Crozier, where an intensive banding and recovery programme is to be maintained. Compared with other skua forms, there is no doubt that *maccormicki* is in an unusually stark environment.

Burton (1968a, b) has provided the most comprehensive account of the biology of skuas in the subantarctic, on *lonnbergi* at Signy Island, including details of postures and sequences of behaviour used in agonistic encounters. Notes on the biology of these species from more temperate habitats are in Downes *et al.* (1959) for Heard Island and Swales (1965) for Gough Island. Tickell (1962) comments on *lonnbergi* as a predator of petrels at several islands. A comparative study of skuas in Antarctica and on the temperate, densely vegetated Chatham Islands was pursued by Young (1978), who found that a high proportion of pairs on Chatham raised both chicks of the pair, the chicks not displaying sibling rivalry at the nest. Study of this population is being continued to provide an explanation for the common occurrence of 3 adult birds at nests.

#### EMPEROR PENGUINS *Aptenodytes forsteri*

Emperor Penguins breed during winter, laying eggs in May and June, and, as individual pairs are not identified with a nest site or colony, individual recognition is always a problem, especially as the brooding birds move about appreciably and in severe conditions huddle into tight amorphous groups losing individual identity. Most colonies are on fast ice linked to the antarctic mainland, difficult or even hazardous of access. It is even difficult to obtain fair counts of numbers. In spite of all these deterrents, considerable research has been carried out on their anatomy and physiology, and on their adaptations for survival and breeding under winter antarctic conditions.

Much of our present understanding of the ecology of the Emperor Penguin is from research conducted since 1952 at the French base at Pointe Géologie, Adélie Land (papers by Prévost, Sapin-Jaloustre, Guillard, Isenmann, Arnaud, Birr, Mougouin and Jouventin), linked to a major banding programme, allowing known-age identification of behaviour and mortality factors. Jouventin (1975) has summarised findings on mortality and population factors there for 1952-1970. No other antarctic studies can match this continuity. Le Maho, Delclitte & Groscolas (1977) record in fine detail temperature relations, metabolic rates and blood plasma constituents of fasting adults, a study only possible in nearby laboratory conditions.

Stonehouse (1953) studied breeding at the single rookery known for the Antarctic Peninsula. Budd (1962) describes techniques used to census rookeries and presents data on penguin numbers through the breeding season, estimating a world population then of 120,000 breeding pairs. Conroy (1975) gives estimates of breeding populations, across a variable number of years, at 7 rookeries, concluding that overall the population number appears stable.

According to Stonchouse (1970) Emperor Penguins have an incubation period of 62 days, and young chicks grow very slowly. The incubation period precludes summer breeding, as chicks could not then fledge at a favourable period for survival, while the slow growth is conditioned by food shortage and adverse temperature conditions. In the view of Isenmann (1971) the length of the 250 day breeding cycle is determined by the need to fit into the sea-ice cycle, from onset of stability to break-out in spring, as this penguin is crucially dependent on this ice for breeding. The birds' behaviour and biology over winter is however marked by the over-riding adaptations that conserve metabolic heat and thus extend the life of the lipid store. It is in this light that the lack of territorial behaviour, which allows huddling, and the facility to move about carrying the eggs and young chicks should be interpreted.

#### OTHER SPECIES

Comparatively little research has been done on other antarctic birds, but there are, however, good accounts of the breeding biology for all species. For example, Maher (1962), Brown (1966), Beck (1970) and Isenmann (1970) for the Snow Petrel *Pagodroma nivea*; Lacan (1971) and Beck & Brown (1972) for Wilson's Storm Petrel *Oceanites oceanicus*; Pinder (1966) and Isenmann (1970b) for the Cape Pigeon *Daption capensis*. Brook & Beck (1972) describe the occurrence of both Antarctic Petrels and Snow Petrels inland on the Theron Mountains, and Parmalee (1977) compares the adaptations of Antarctic Terns and Arctic Terns *Sterna paradisaea* to antarctic ecosystems. Watson *et al.* (1971) and Watson (1975) provide comprehensive bibliographies for all species.

#### CONCLUSION

This review has briefly touched on some of the work done in antarctic ornithology over the past two decades, since the great upsurge of effort heralded by the International Geophysical Year (IGY) 1958-59. The results achieved reflect an enormous commitment to research under difficult conditions — research made possible by the availability of safe and rapid transport.

Antarctic ornithology has matured astonishingly quickly to its present sophisticated, and increasingly laboratory oriented, status. It is, however, best developed in its details; the central problem of the long term regulation of bird numbers in the Antarctic region is still little understood. A major research effort is needed into factors determining abundance and distribution of species. What is missing especially is information on overwintering and feeding strategies. Without this information it is simply not possible to complete the accounts of species' biology and population dynamics.

Scientists and administrators carry a heavy responsibility to ensure that these unique assemblages of species survive into the future. They are at risk at present from the introduction of pollutants and avian diseases, but any economic exploration of Antarctica would greatly increase the risk of local extinctions.

Overall, the last 20 years have been ones of great achievement. Levick (1915) wrote "The habits of the Adélie Penguin have been dealt with from

time to time by different writers, but the information to be had from these is fragmentary and misleading". At least for this species this is no longer true.

*Acknowledgement*: I gratefully acknowledge the help given by S. M. Martin, J. M. Davenport and P. M. Young in the preparation of this review.

#### References:

- Ainley, D. G. 1975a. Development of reproductive maturity in Adélie Penguins. In Stonehouse, B. (ed) 1975: 139-157.
- Ainley, D. G. 1975b. Displays of Adélie Penguins: a reinterpretation. In Stonehouse, B. (ed) 1975: 503-534.
- Ainley, D. G. 1978. Activity patterns and social behaviour of non-breeding Adélie Penguins. *Condor* 80: 138-146.
- Ainley, D. G. & Le Resche, R. E. 1973. The effects of weather and ice conditions on breeding in Adélie Penguins. *Condor* 75: 235-239.
- Ainley, D. G. & Emison, W. B. 1972. Sexual size dimorphism in Adélie Penguins. *Ibis* 114: 267-271.
- Andersson, M. 1973. Behaviour of the Pomarine Skua *Stercorarius pomarinus* Temm. with comparative remarks on Stercorariinae. *Orn. Scand.* 4: 1-16.
- Austin, O. L. (ed). *Antarctic Bird Studies*. Antarctic Res. Ser. 12: 1-262. Washington.
- Baker, J. R. 1973. Penguin and skua studies at Hallett Station. *Antarctic J. U.S.* 8: 200-201.
- Beck, J. R. 1970. Breeding seasons and moult in some smaller Antarctic petrels. In Holdgate, M. W. *Antarctic Ecology* 1: 542-550. Academic Press: London.
- Beck, J. R. & Brown, D. W. 1972. The biology of Wilson's storm petrel, *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. *Sci. Rep. Brit. Antarctic Surv.* 69: 1-54.
- Behn, F., Goodall, J. D., Johnson, A. W. & Phillippi, B. 1955. The geographic distribution of the Blue-eyed Shags *Phalacrocorax albiventer* and *Phalacrocorax atriceps*. *Auk* 75: 6-13.
- Bonner, W. N. 1964. Polygamy and super-normal clutch size in the Brown Skua, *Catharacta skua lombergi* (Mathews). *Bull. Brit. Antarctic Surv.* 3: 41-47.
- Brook, D. & Beck, J. R. 1972. Antarctic petrels, snow petrels and south polar skuas breeding in the Theron Mountains. *Bull. Brit. Antarctic Surv.* 27: 131-137.
- Bourne, W. R. P. & Warham, J. 1966. Geographical variation in the giant petrels of the genus *Macronectes*. *Ardea* 54: 45-67.
- Brown, D. A. 1966. Breeding biology of the Snow Petrel *Pagodroma nivea* (Forster). *ANARE Sci. Rep.* B (1) 89: 63.
- Budd, G. M. 1962. Population studies in rookeries of the Emperor Penguin *Aptenodytes forsteri*. *Proc. Zool. Soc. Lond.* 139: 265-288.
- Burton, R. W. 1968a. Breeding biology of the Brown Skua, *Catharacta skua lombergi* (Mathews) at Signy Island, South Orkney Islands. *Bull. Brit. Antarctic Surv.* 15: 9-28.
- Burton, R. W. 1968b. Agonistic behaviour of the Brown Skua, *Catharacta skua lombergi* (Mathews). *Bull. Brit. Antarctic Surv.* 16: 15-39.
- Carrick, R. & Ingham, S. E. 1967. Antarctic sea birds as subjects for ecological research. *JARE Sci. Rep.* Special Issue 1: 151-184.
- Carrick, R. & Ingham, S. E. 1970. Ecology and population dynamics of Antarctic sea birds. In Holdgate, M. W. (ed.) *Antarctic Ecology* 1: 505-525. Academic Press: London.
- Conroy, J. W. H. 1975. Recent increases in penguin populations in Antarctica and the Subantarctic. In Stonehouse, B. (ed.) 1975: 321-336.
- Derksen, D. V. 1977. A quantitative analysis of the incubation behaviour of the Adélie Penguin. *Auk* 94: 552-566.
- Devillers, P. 1977. The skuas of the North American Pacific coast. *Auk* 94: 417-429.
- Devillers, P. & Terschuren, J. A. 1978. Relationships between the Blue-eyed Shags of South America. *Gerfaut* 68: 53-86.
- Downes, M. C., Ealey, E. H. M., Gwynn, A. M. & Young, P. S. 1959. The birds of Heard Island. *Rep. Aust. Nat. Antarctic Res. Exped.* 1B: 1-135.
- Eklund, C. R. 1961. Distribution and life history studies of the South Polar Skua. *Bird Banding* 32: 187-223.

- Emlison, W. B. 1968. Feeding preferences of the Adélie Penguin at Cape Crozier, Ross Island. *Antarctic Res. Serv.*, Washington 12: 191-212.
- Emlen, J. T. & Penney, R. L. 1966. The navigation of penguins. *Scient. Amer.* 215: 104-113.
- Falla, R. A. 1964. Distribution patterns of birds in the Antarctic and high-latitude Subantarctic. In Carrick, R., Holdgate, M. & Prévost, J. (eds) *Biologie Antarctique*: 367-376. Hermann: Paris.
- Furness, R. W. 1978. Energy requirements of seabird communities: a bioenergetic model. *J. Anim. Ecol.* 47: 39-53.
- Gain, L. 1914. Oiseaux antarctiques. Deuxième expédition antarctique française (1908-1910). *Sci. Naturelles*: Documents Scientifiques. Maison: Paris.
- Guthrie-Smith, H. 1925. *Bird Life on Island and Shore*. Blackwood: Edinburgh.
- Hamilton, J. E. 1934. The sub-antarctic forms of the Great Skua (*Catharacta skua skua*). *Discovery Rep.* 9: 161-174.
- Issenmann, P. 1970a. Contribution à la biologie de reproduction du Petrel des Neiges (*Pagodroma nivea* Forster) le probleme de la petite et de la grande forme. *L'Oiseau et R.F.O.* 40 (Special Number): 99-134.
- Issenmann, P. 1970b. Note sur la biologie de reproduction comparée des damiers du cap Daption capensis aux orcades du sud et en Terre Adélie. *L'Oiseau et R.F.O.* 40 (Special Number): 135-141.
- Issenmann, P. 1971. Contribution à l'ethologie et à l'écologie du Manchot Empereur *Aptenodytes forsteri* (Gray) à la colonie de Pointe Geologie (Terre Adélie). *L'Oiseau et R.F.O.* 41 (Special Number) 9-64.
- Johnstone, G. W. 1979. Agonistic behaviour of the giant petrels *Macronectes giganteus* and *M. halli* feeding at seal carcasses. *Emu* 79: 129-132.
- Jouventin, P. 1975. Mortality parameters in Emperor Penguins, *Aptenodytes forsteri*. In Stonehouse, B. (ed.) 1975: 435-446.
- Lacan, F. 1971. Observations écologiques sur le petrel de Wilson (*Oceanites oceanicus*) en Terre Adélie. *L'Oiseau et R.F.O.* 41 (Special Number): 65-89.
- Le Maho, Y., Delclitte, P. & Chatonnet, J. 1976. Thermoregulation in fasting emperor penguins under natural conditions. *Amer. J. Phys.* 231: 913-922.
- Le Morvan, P., Mougou, J. L. & Prévost, J. 1967. Ecologie du skua Antarctique (*Stercorarius skua maccormicki*) dans l'Archipel de Pointe Geologie (Terre Adélie). *L'Oiseau et R.F.O.* 37: 193-200.
- Le Resche, R. E. & Sladen, W. J. L. 1970. Establishment of pair and breeding site bonds by young known-age Adélie Penguins (*Pygoscelis adeliae*). *Anim. Behav.* 18: 517-526.
- Levick, G. M. 1915. *Natural History of the Adélie Penguin*. *Nat. Hist. Rep.* British Antarctic "Terra Nova" Expedition 1910 1: 55-84.
- Maher, W. J. 1962. Breeding biology of the Snow Petrel near Cape Hallett, Antarctica. *Condor* 64: 488-499.
- Maher, W. J. 1966. Predation's impact on penguins. *Nat. Hist.* (New York) 75: 42-51.
- Moynihan, M. 1959. A revision of the Family Laridae (Aves). *Amer. Mus. Novit.* 1928: 41 pages.
- Moynihan, M. 1962. Hostile and sexual behaviour patterns of South American and Pacific Laridae. *Behaviour Supplement* 8.
- Müller-Schwarze, D. 1968. Circadian rhythms of activity in the Adélie Penguin (*Pygoscelis adeliae*) during the austral summer. *Antarctic Res. Ser.* (Washington) 12: 133-149.
- Müller-Schwarze, D. & Müller-Schwarze, C. 1971. Antipredator and social behaviour in Adélie Penguins (*Pygoscelis adeliae*). *Antarctic J. U.S.* 6: 99-100.
- Murphy, R. C. 1936. *Oceanic Birds of South America*. Amer. Mus. Nat. Hist., New York.
- Oelke, H. 1975. Breeding behaviour and success in a colony of Adélie Penguins, *Pygoscelis adeliae*, at Cape Crozier, Antarctica. In Stonehouse, B. (ed) 1975: 363-395.
- Parmalee, D. F. 1977. Adaptations of Arctic terns and Antarctic terns within Antarctic ecosystems. In Llano, G. A. (ed) *Adaptations within Antarctic Ecosystems*: 687-702.
- Parmalee D. F., Bernstein, N. & Neilson, D. 1978. Impact of unfavourable ice conditions on bird productivity at Palmer Station during the 1977-78 field season. *Antarctic J. U.S.* 13: 146.
- Penney, R. L. 1968. Territorial and social behaviour in the Adélie Penguin. *Antarctic Res. Serv.* (Washington) 12: 83-131.

- Pinder, R. 1966. The Cape Pigeon, *Daption capensis* Linnaeus, at Signy Island, South Orkney Islands. *Bull. Brit. Antarctic Surv.* 8: 19-47.
- Prince, P. A. & Payne, M. R. 1979. Current status of birds at South Georgia. *Brit. Antarctic Surv. Bull.* 48: 103-118.
- Procter, D. L. 1975. The problem of chick loss in the South Polar skua *Catharacta macormicki*. *Ibis* 117: 452-459.
- Reid, B. E. 1964. The Cape Hallett Adélie Penguin rookery — its size, composition and structure. *Rec. Domin. Mus. N.Z.* 5: 11-37.
- Salomonsen, F. 1976. The South Polar skua *Stercorarius macormicki* Saunders in Greenland. *Dan. Ornith. Foren. Tidsskr.* 703: 81-89.
- Schnell, G. D. 1970. A phenetic study of the Suborder Lari (Aves). *Syst. Zool.* 19: 35-57; 264-302.
- Sladen, W. J. L. 1958. The Pygoscelid Penguins. I. Methods of study; II. The Adélie Penguin. *Falkl. Isl. Dep. Surv. Sci. Rep.* 17: 1-97.
- Sladen, W. J. L., Le Resche, R. E. & Wood, R. C. 1968. Antarctic avian population studies 1967-68. *Antarctic J. U.S.* 3: 247-260.
- Spellerberg, I. F. 1971a. Aspects of McCormick skua breeding biology. *Ibis* 113: 357-363.
- Spellerberg, I. F. 1971b. Breeding behaviour of the McCormick skua *Catharacta macormicki* in Antarctica. *Ardea* 59: 189-230.
- Spellerberg, I. F. 1975. The predators of penguins. In Stonehouse, B. (ed) 1975: 413-434.
- Spurr, E. B. 1974. Individual differences in aggressiveness of Adélie Penguins. *Anim. Behav.* 22: 611-616.
- Spurr, E. B. 1975a. Communication in the Adélie Penguin. In Stonehouse, B. (ed) 1975: 449-501.
- Spurr, E. B. 1975b. Behaviour of the Adélie Penguin chick. *Condor* 77: 272-280.
- Spurr, E. B. 1975c. Breeding of the Adélie Penguin *Pygoscelis adeliae* at Cape Bird. *Ibis* 117: 324-338.
- Spurr, E. B. 1975d. Orientation of Adélie Penguins in their territories. *Condor* 77: 335-337.
- Spurr, E. B. 1978. Diurnal activity of Adélie Penguins *Pygoscelis adeliae* at Cape Bird. *Ibis* 120: 147-152.
- Stonehouse, B. 1953. The Emperor Penguin *Aptenodytes forsteri*. *Falkl. Isl. Dep. Surv. Sci. Rep.* 6: 33 pages.
- Stonehouse, B. 1956. The Brown Skua *Catharacta skua lomnbergi* (Mathews) of South Georgia. *Falkl. Isl. Dep. Surv. Sci. Rep.* 14: 25 pages.
- Stonehouse, B. 1963. Observations on Adélie Penguins (*Pygoscelis adeliae*) at Cape Royds, Antarctica. *Proc. XIII Int. Orn. Congr.* 1962: 766-779.
- Stonehouse, B. 1965. Birds and Mammals. In Hatherton, T. (ed) *Antarctica*: 153-186. Reed: Wellington.
- Stonehouse, B. 1967. The general biology and thermal balances of penguins. *Adv. Ecol. Res.* 4: 131-196.
- Stonehouse, B. 1970. Adaptations in polar and subpolar penguins (*Spheniscidae*). In Holdgate, M. W. (ed) *Antarctic Ecology* 1: 526-54. Academic Press, London.
- Stonehouse, B. (ed) 1975. *The Biology of Penguins*. The Macmillan Press, London.
- Swales, M. K. 1965. The sea birds of Gough Island. *Ibis* 107: 17-42, 215-229.
- Taylor, R. H. 1962. The Adélie Penguin *Pygoscelis adeliae* at Cape Royds. *Ibis* 104: 176-204.
- Tenaza, R. 1971. Behaviour and nesting success relative to nest location in Adélie Penguins (*Pygoscelis adeliae*). *Condor* 73: 81-92.
- Tickell, W. L. N. 1962. The Dove Prion *Pachyptila desolata* Gmelin. *Falkl. Isl. Dep. Sci. Rep.* 14: 55 pages.
- Todd, F. S. 1978. Establishment of a high antarctic penguin colony and controlled environment breeding of Adélie Penguins (*Pygoscelis adeliae*). *Antarctic J. U.S.* 13: 153-154.
- Trillmich, F. 1978. Feeding territories and breeding success of south polar skuas. *Auk* 95: 23-33.
- Voisin, J. F. 1970. On the specific status of the Kerguelen shag and its affinities. *Notornis* 17: 286-290.
- Watson, G. E. 1975. *Birds of the Antarctic and Sub-antarctic*. Antarctic Res. Ser. Amer. Geophys. Union, Washington: 350.

- Watson, G. E., Angle, J. P., Harper, P. C., Bridge, M. A., Schlatter, R. P., Tickell, W. L. N., Boyd, J. C. & Boyd, M. M. 1971. *Birds of the Antarctic and Subantarctic*. Antarctic Map Folio Series, Folio 14. Amer. Geograph. Soc.
- Wood, R. C. 1971. Population dynamics of breeding south polar skuas of unknown age. *Auk* 88: 805-814.
- Yeates, G. W. 1971. Diurnal activity in the Adélie Penguin (*Pygoscelis adeliae*) at Cape Royds, Antarctica. *J. Nat. Hist.* 5: 103-112.
- Yeates, G. W. 1975. Microclimate, climate and breeding success in Antarctic penguins. In Stonehouse, B. (ed) 1975: 397-409.
- Young, E. C. 1963a. The breeding behaviour of the south polar skua *Catharacta maccormicki*. *Ibis* 105: 203-233.
- Young, E. C. 1963b. Feeding habits of the south polar skua *Catharacta maccormicki*. *Ibis* 105: 301-318.
- Young, E. C. 1970. The techniques of a skua-penguin study. In Holdgate, M. W. (ed). *Antarctic Ecology* 1: 568-584. Academic Press: London.
- Young, E. C. 1972. Territory establishment and stability in McCormick's skua. *Ibis* 114: 234-244.
- Young, E. C. 1978. Behavioural ecology of *lombergi* skuas in relation to environment on the Chatham Islands, New Zealand. *N.Z. J. Zool.* 5: 401-416.

Address: Professor E. C. Young, Zoology Department, University of Auckland, Private Bag, Auckland, New Zealand.

© British Ornithologists' Club.

## Ornithology in Canada in the 20th Century: a capsule overview

by Henri Ouellet & W. Earl Godfrey

The study of birds has had a long tradition in Canada but it was not until the turn of the century that an important work on the bird fauna of the entire country became available (*Catalogue of Canadian Birds*, 1909, J. & J. M. Macoun). This landmark, which brought together the results of early surveys in various regions, as well as previously published data, precluded more comprehensive and detailed works.

Early in the century the National Museum of Canada, in Ottawa, became the major centre of Canadian ornithological research mainly through the efforts of P. A. Taverner, ornithologist with the Museum from 1911 to 1942. Taverner left an impressive legacy through his numerous ornithological investigations. In addition to conducting a vigorous programme in bird distribution and taxonomy, he expanded the collection from about 4000 to more than 30,000 specimens during his tenure. He conceived a remarkable system of maps and index reference cards to record bird distribution, still currently in use. He recognised the need for extensive field surveys and organised many field parties to various parts of the country to obtain specimens and first hand distribution data. His publications number about 300. He authored *Birds of Canada* (1934) and its predecessors *Birds of Eastern Canada* 1919 and *Birds of Western Canada* 1916, which became the basic references on Canadian birds for several decades. They greatly popularised ornithology at a time when there was little general interest in birds in Canada, outside naturalist groups. His concern for conservation made him instrumental in the creation of Point Pelee National Park and the Bonaventure